Life-Histories and Larval Habits of the Tiger Beetles (*Cicindelidæ*).

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(Plates 23–26.)

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I. Introduction.

During the past quarter century, the consideration of life-histories and habits as a basis for experimental work and for the study of distribution, variation and other evolutionary topics has been far too much neglected. In the study of variation, investigators have too often collected large numbers of specimens, arranged them in classes, calculated indices, constructed curves, and drawn conclusions regarding the direction of evolution without knowing the life-history of the form and without determining whether the characters studied are easily modified by varying conditions during development, or whether they change during the life of the individual.

Recent studies of the variation of the potato beetle from generation to generation, by Tower, and of seasonal changes in the number of ray flowers of certain *Compositæ*, by Tower, Shull and others, have called attention to the great liability to error in investigations conducted in this manner.

An analysis of the environmental conditions of an organism during development cannot be made until the complete life-cycle is known. The responses and habits of the adult Tiger Beetles at the time of laying, as we shall note later, and of the larvæ, especially at the time of preparation for pupation, determine in many cases the conditions under which later stages must be passed. In the pupal and prepupal stages at least, these organisms are sensitive to external stimuli.

It is my purpose to present in this paper the general outlines of those activities and reactions connected with reproduction, which have a special bearing on the more general papers to follow. The succeeding papers will deal with the following topics :—distribution, variation, the effects of varying environmental conditions during development, an analysis of the colour patterns, a discussion of race tendencies of the genus *Cicindela*, and the bearing of the whole on the problem of evolution. The data on the selection of habitat and on colour-changes herein mentioned, will be presented in detail in another connection.

II. Previous accounts of Larvæ and Life-Histories.

The larva and larval habits of a European species, *Cicindela campestris*, Linn., were described by the early writers on natural history and are better known than those of any other member of the group. Geoffroy gave a general account in 1762, to which details were added by Desmarest in 1804 and Westwood in 1838. Blisson described the pupa and the last part of the life-history in 1848, and Enock completed the account in 1903. The latter contributed a description of the eggs, the open burrows in which they are laid, and a detailed account of the burrowing habits of the larvæ. Several other larvæ, pupæ, etc., chiefly European, have been described. Ponselle gave an account of the egg and egg-laying habits of *C. flexuosa*, Fabr., but stated that he was unable to secure any larvæ from eggs removed from the soil, because of fungus attacks.

Larvæ.

The notable characters of the larvæ are the head and prothorax, which close the burrow when the animal is waiting for prey, and the hooks and spines of the fifth abdominal segment which enable it to move up and down in the burrow and prevent large prey from dragging it out. Descriptions of the structures of these larvæ are easily accessible in text-books of entomology, &c. Enock's account of their habits and movements is detailed, accurate, and in a general way applies to the whole group.

Burrows—Soil Inhabiting Forms.

The burrows are not so well known as the larvæ. They differ more in different species than the larvæ themselves. They are usually cylindrical and have a circular opening at the surface. The edge of the opening is slightly rounded and perfectly smooth. Surrounding it is a circular area which extends outward, from the edge of the opening for a distance a little less than the equivalent of the diameter of the burrow itself. This area the animal keeps smooth and clean by removing all loose earth and packing the particles of soil with its mandibles. This smooth area and rounded edge almost always serve to distinguish the burrows of *Cicindelidæ* from those of other animals. Tiger-beetle burrows occur in horizontal or vertical surfaces, or surfaces sloping at any angle between these two extremes. The general direction of the burrows is vertical or at right angles to the surface, all apparently depending upon the habit of the particular species. Those of some species are curved, as for example *C. hybrida* Linn. (Lesne), or straight like those of *C. campestris*. The depth varies from a little more than the equivalent of the length of the animal's body, in the case of larvæ found in hard soil, to 1·25 metres in the case of larvæ mentioned by Criddle as occurring at Aweme, Manitoba ; it is related to the character of the soil, temperature, the distance to ground-water, and possibly other factors.

Arboreal Forms.

There are several genera of tree dwellers. Their young stages are unknown except in *Collyris*. R. Shelford has recently described one of these in detail. The larva has its burrow in the stems of the coffee plant and is an agricultural pest in the East Indies. Its method of food-taking is like that of the larvæ of *Cicindela*.

III. Methods of rearing Larvæ.

Cicindelidæ have always been regarded as very difficult to rear. I have had no success outside of a well ventilated glass-roofed vivarium. The adults of a given species were put in a cage containing the soil which they frequent, or better, that which their larvæ inhabit. Most of the species here considered can be induced to lay without difficulty.

For rearing larvæ in large numbers from the last stage to maturity, a screen bottomed box containing sand (or sandy soil) can be placed over other moist soil which will maintain any desired degree of moisture. If well cared for, even the species that leave their holes when conditions are not favourable, can be reared in numbers by this method without great mortality. It is well to tack strips of tin on the edge of such a box, allowing them to project 3 to 5 cm. over the inside ; this will prevent the larvæ from escaping.

For the study of larval habits, cages were made of glass plates separated by glass tubing of a diameter corresponding to the width of the prothorax of the species to be studied, and cemented together with paraffin of a high melting-point. Bottoms were made of cloth saturated with paraffin (by first wetting in xylol or turpentine) to prevent decay, and fastened in place with hard paraffin. Straight cylindrical Welsbach lamp chimneys were also used for this purpose. The soil, if well packed, will stay in these and the moisture may be maintained by capillarity, through additions from below.

Pupæ were often kept in Syracuse watch-glasses lined with moist filter-paper, through the greater part of the pupal life, with a relatively low mortality. The filter-paper should be moistened with 3 per cent. hydrogen peroxide from time to time ; this may be dropped directly on the bodies of the pupæ and will help to keep down the fungi which are the chief cause of trouble in all these studies.

All larvæ and adults were fed with small pieces of lean meat which were placed in the burrows or cages every day.

IV. Life-Histories of the Species occurring near Chicago.

Twelve races have been studied ; all but one have been reared to at least the second larval stage. Extensive field observations connected with the collecting and rearing of three to four thousand individuals from the last larval stage to maturity, have served to verify and complete the accounts. The races and species considered are :—**purpurea*, Oliv.; *purpurea*, Oliv. sub-species *limbalis*, Klg.; *formosa*, Say, sub-species *generosa*, Dj.; *duodecimguttata*, Dj.; *duodecimguttata*, Dj. sub-species *repanda*, Dj.; *tranquebarica*, Herbst; *scutellaris*, Say, aber. *Lecontei*, Hald.; *hirticollis*, Say; *sexguttata*, Fab.; *punctulata*, Oliv.; *lepida*, Lec.; and *cuprascens*, Lec.

For convenience I shall discuss in detail the life-history and larval habits of *C. purpurea*. The accounts of the remaining species will be comparative, and the points in which they differ from that of *purpurea* will be especially noted. Unless otherwise stated, it is to be understood that the length of the various stages is approximately the same as in *purpurea*:—Period of incubation, 2 weeks; first larval stage, 4 to 5 weeks; second larval stage, 5 to 7 weeks; pupal and prepupal stages, each 2 to 3 weeks.

Cicindela purpurea.

The Ovipositor.—The ovipositor (Pl. **23.** figs. 1, 2 & 3) of *Cicindela purpurea* is made up of abdominal segments 8, 9 and 10 and their appendages. The posterior part of the seventh and anterior part of the eighth segment are soft and pliable, serving to permit the entire posterior end of the abdomen to be withdrawn into the segments in front, as is the case in many Coleoptera. The posterior half of the eighth segment possesses on its dorsal and ventral sides respectively, a chitinized plate. These two plates are separated by a soft portion representing the pleuron, which makes it possible for them to approach each other very closely. The ventral plate is prolonged backward in the form of a pair of pointed projections, representing the gonapophyses of the eighth segment. On the ventral side of the ninth segment is borne a pair of movable, strongly chitinized gonapophyses, which are used in digging into the soil for egg-laying (Pl. **23.** figs. 1, 2 & 3). Also arising from this segment (9th), as can be followed in a series of pupæ, are to be found an outer pair of appendages. In the adult, these lie dorsal and somewhat separated from the others, at the sides of the tenth segment which is without appendages. The outer gonapophyses of the ninth segment and the tenth segment are covered with hairs, which are in all probability sensory. In the pupa, the outgrowths which are to form the movable gonapophyses are present at the moulting of the larval skin and stand out as well differentiated parts.

Mating and Egg-laying.—The mating and egg-laying habits were observed in animals in captivity in the latter part of April, 1904, 1905, and 1906. Specimens captured at Lyons, Ill., April 22, 1904, were carefully studied.

* The nomenclature used in this paper is to be found in Horn's "Systematischer Index der Cicindeliden," Deutsch. Ent. Zeit., Feb. 1905, Supplement. *C. scutellaris*, Say, however, stands in that publication as *obscura*, Say, the corresponding change having been made by the same author in a later publication.

They copulated some time during three or four days following their capture and the first eggs were found April 26th. There appear to be no special courting movements ; a male quickly seizes a female by the thorax with his heavy mandibles and rests with the ventral side of his body against the dorsal side of the female, his legs extended freely at the sides. He may remain in position for a long time and finally succeed in copulating with the female. If, because of being disturbed, he leaves her, he has been known to return to the same one to the exclusion of other females that were present. Some days after fertilization (the length of time is difficult to determine because of the continued copulation or attempts at copulation on the part of the male) the female seeks a place to lay her eggs. She holds the anterior part of the body as high as possible and, extending the posterior part of the abdomen (ovipositor), she digs a vertical hole with the gonapophyses of the abdomen, from 7 to 9 mm. in depth. She tries the soil by making holes without laying any eggs. About fifty eggs are laid, singly and large end uppermost (Pl. **23.** fig. 4), in such uncovered holes by one female. Whether or not more than one lot of eggs is laid by one female has not been definitely determined, but it is quite improbable from all evidence at hand.

The method of egg-laying is essentially like that found in *C. campestris* by Enock and in *C. flexuosa* by Ponselle.

The Egg.—The egg is shaped like a hen's egg but somewhat more elongated; 2 mm. long, 1 mm. in diameter at the small end and $1\frac{1}{5}$ mm. at the large end. It is of a clear, translucent cream-colour and slightly shiny ; the chorion is very easily ruptured (Pl. **23.** figs. 5 & 6).

About two weeks after the eggs were laid, small larvæ appeared (May 8, 9 and 10 in 1904). Those in the dryer parts of the soil appeared only after the soil had been moistened.

First Larval Stage.—The larva at hatching is much like the later stages (Pl. **23.** fig. 7). The abdomen is much wrinkled between the more strongly chitinized plates, bringing them into close contact. The width of the prothorax is $1\frac{1}{4}$ mm. Soon after hatching, the larva makes its way to the surface, packing the soil so as to form a cylindrical burrow with a diameter a little greater than that of its prothorax. This burrow corresponds in position to the hole made by the ovipositor and at first is no deeper. The larva soon digs to a depth of 10 to 15 cm.

After feeding for three to four weeks (fig. 8), the larva closes the mouth of the burrow with soil and goes to the bottom and moults, returning again to the surface at the end of from five to seven days.

Second Larval Stage.—The head, prothorax, appendages and strongly chitinized plates are larger (fig. 9) ; the size of the abdomen is essentially the same as just before moulting but the cuticula is again wrinkled. The larva makes its way to the surface probably by removing the soil from above, thus enlarging the hole and allowing the loosened earth to fall to the bottom.

Under favourable conditions this stage lasts about five weeks. The time is doubtless modified by temperature and food conditions, as some individuals require longer. The activities connected with the second larval moult are the same as those connected with the first.

Last Larval Stage.—The changes are essentially the same as in the first moult; the diameter of the prothorax is 3½ to 4 mm. (Pl. **23**. figs. 10 & 11).

During the latter part of August and the month of September the larvæ disappear, closing the outer end of their burrows and going to the bottom to remain until spring. (In captivity they were kept as nearly as possible under normal conditions and the survivors were found with their holes opened in the early part of April.) They feed until the middle of June, when they fill the upper part of the burrows. Each then constructs an ovoid cavity (fig. 13) near the bottom of its burrow. Having carefully packed and smoothed the soil forming the wall of this cell with its mandibles and the ventral side of its head, each larva remains at rest with the body leaning against one of the sides of the pupal cavity. The head is uppermost and the animal gradually becomes less and less active as time goes on. At the end of two or three weeks it is almost incapable of moving the legs. The abdomen gradually thickens and becomes a clear, characteristic, cream colour, due to internal changes. The tubercles of the first five abdominal segments of the pupa (fig. 12) can be seen through the larval skin. They are folded toward the centre of the back.

Pupal Ecdysis.—A few days after the conditions just mentioned have become apparent, the pupa emerges from the larval skin. The cuticula splits in the mid-dorsal line of the thoracic segments and the head; the split on the head bifurcates, following the suture at the posterior side of the clypeus.

The process of shedding the skin requires only a few minutes and has been seen in the variety *limbalis.* It is accomplished by contractions of the ventral body-muscles which tend to elongate the dorsal side and bring the old skin under tension. The thoracic portions of the body are the first to emerge; the skin meanwhile slips backward on the abdomen and the head is gradually withdrawn, usually becoming free before the abdomen. The abdomen is freed by its later movements. The pupa possesses very few bristles that could assist in the removal of the exuvium. The only ones are a few on the margins of the pronotum and several long ones on each abdominal tubercle. The bristles of the tubercles together with the tubercles themselves obviously assist in working the exuvium from the abdomen. An exuvial fluid is apparently present, and this together with the great expansion of the wings and appendages is sufficient to insure safe emergence.

The Pupa.—At the time of emergence the pupa is only a little shorter than the larva, but it soon contracts and assumes the form shown in fig. 12. As has been noted by former workers, the dorsal tubercles serve to hold the body away from the substratum on which it rests.

At emergence, the eyes are pale brown and gradually become darker by the development of the iris and retinal pigment, until the end of about ten days when the process appears to be complete. Differentiation of the appendages of the adult begins at their distal ends. Cuticular pigment develops only when the cuticula is mature. The appearance of pigment is coincident with final hardening. At the end of twelve days pigment has appeared on the tips of the mandibles and a little later on the tips of the mandibular teeth. It proceeds from these toward the proximal portions, and by the 13th or 14th day the process is complete. On or about the 13th day the tarsal claws are pigmented, and a day or two later the proximal portion of the tibia shows pigment which moves toward the more distal portions. Coincident with the development on the tibia, pigment appears on the outer border of the trochanters and later develops at the attachment of the principal muscles and tendons of the leg (Pl. 24. fig. 14).

The Last Ecdysis.—The first movement possible in the pupa is that of the tarsal claws. The legs, early in the process of moulting, are moved outward from the body and slightly straightened. For this the trochanter muscles and the muscles of the femur are used. Their attachments are hardened and pigmented and movement is accordingly possible. By vigorous movements, especially of the legs and mandibles, the pupal skin is ruptured and the continuation of the movement frees the imago.

The bristles of the adult assist in the removal of the exuvium. Their arrangement is well illustrated in the legs (Pl. 24. fig. 14) and other appendages, where they occupy much space inside the pupal skin. This function of the bristles was suggested by Miall and Denny in their work on the Cockroach.

The Imago.—After emergence, the imago remains in the cell for several days, the pigment of the body meanwhile developing. The only specimen of *purpurea* that was brought to maturity emerged on August 11th and about eighteen hours afterwards had apparently reached an adult colour. It lived for ten days longer, during which time it underwent a series of colour-changes that will be described elsewhere.

In nature, adults appear in the latter part of each August. They feed during the early fall, and in early October dig holes in some little bare bank in a meadow or go into the hole of some other insect for hibernation. They have been dug, in late October, from such situations, being apparently helpless from the cold. Specimens hibernating in captivity appeared in the latter part of March. They reach sexual maturity late in April, lay eggs and die.

Summary and Comparison.—The life-history of *Cicindela purpurea* may be summarized as follows:—The eggs are laid in May; larvæ reach the last stage in August, hibernate, begin to feed again in April and pupate in July; the adults emerge in August, feed for a time, hibernate and come out in the second spring still sexually immature, reach maturity in the first warm days of April and lay eggs and die. The larval life lasts from twelve to thirteen months and the adult life ten months—two years between generations.

The essential features of Enock's account of the life-history of *C. campestris* are as follows :—The larvæ live through two winters, deepening their holes each autumn and appearing again in the spring. An oblique pupal cavity is made in August. The adults emerge in autumn, remain through the third winter in the pupal cell in an inactive state and come out in the spring of the third year.

He does not state the number of larval stages nor did he breed any of the insects. The larvæ of a number of North American species live over only one winter and the last larval stages of two generations overlap, so that one finds very young larvæ and mature larvæ of this stage in July. From field observations alone one might conclude that the larvæ live over two winters.

CICINDELA PURPUREA, subsp. LIMBALIS.

The adults appear later in the spring than those of *purpurea* and the egg-laying takes place in June. The female, after fertilization, selects a place to deposit eggs (they are laid in clay) by first trying the soil as I have described for *purpurea*. In my cages the larvæ were not carried further than the second stage, but they have been observed in nature in a habitat where only this species occurs ; from this locality, about six hundred larvæ have been collected and reared to maturity.

In the early part of September, only larvæ of the first and second stages can be found, and later in the autumn the first stage becomes very scarce. They pass the winter chiefly in the second stage and appear in the latter part of May or the first of June when they enter the last stage. The larval burrows enter nearly at right angles to the surface of the steep clay bank in which the larvæ live, and curve into a nearly horizontal position at the inner end ; the depth is from 7·5 to 10 cm. A chimney-like structure about 6 mm. in height is usually built up at the mouth of the hole with clay removed from the bottom. The pupal cell is made by enlarging and shifting the inner end of the burrow (Pl. **24**. fig. 18). They enter the prepupal stage during the first two weeks of July.

Some of the adults appear in the early part of August in some years and undergo a series of colour-changes. The stragglers of the former generation may be present in small numbers in the early part of August and continue mixed with the young ones as late as September. The adults hibernate and appear in the spring, reaching sexual maturity in June, about a month later than does the true *purpurea*.

Weather Conditions and Time of Appearance.—The latter part of July, 1905, was very wet and warm at Chicago and I found fresh *limbalis* in numbers at Glencoe on August 3rd. July, 1906, on the contrary, was very dry and I was unable to get any until September 5th, at which time they were very much scattered. The specimens reared from larvæ brought into the vivarium emerged as in former years. These insects are unable to dig their way out until the soil is thoroughly wet. Leng has observed a similar variation in the time of appearance of another variety.

CICINDELA FORMOSA, subsp. GENEROSA.

This species lays its eggs in May and June, in fresh sand. Eggs are difficult to secure and have not been studied. In my cages larvæ appeared June 24th. The head and prothorax are much larger than those of any of the other species here considered and possess a colour pattern (Pl. **24.** fig. 16). The burrow is entirely different from those described above.

The Burrow.—The main part of the burrow is from 30 to 50 cm. deep and vertical throughout the greater part of its course. At a distance from the opening equal to two-thirds of the length of the animal's body (Pl. **25.** figs. 22–24), it curves sharply to a horizontal position like a stove-pipe elbow and opens into the side of a pit. The edge of the pit usually overhangs the mouth of the burrow in such a manner as to make it almost invisible. The head and prothorax of a larva of the first stage are almost as large as those of the last stage of some other species (1·75 mm.). The larvæ are always to be found in sand that is slightly shifting. The great size of the hole would cause it to fill up with the sand moved about by the wind and thus make the animal a great amount of labour. Each larva cements the sand-grains slightly with saliva. Accordingly its hole and pit near the opening are quite firm and the wind does not ordinarily disturb them. The pit may fill and be almost obliterated by the action of either wind or rain ; the burrow, however, remains undisturbed, except possibly when the rain is very heavy. This type of burrow possesses advantages in securing prey ; the pit acts as a pitfall for small animals. It is more elaborate than that of *C. hybrida* (a European species), described by Lesne, in which the pit and curvature of the burrow are relatively imperfect (Pl. **24.** fig. 17).

In my cages, the larvæ reached the third stage in the latter part of August. They all disappear in the field by the first of October and reappear again in the spring. In the latter part of June and the first half of July, they go into the prepupal stage, each in an oblique side cavity about 10 cm. below the surface (Pl. **25.** fig. 24) : the upper part and much of the lower part of the hole is filled with the sand that is taken from this elliptical cavity. The adults of a given generation are not found so abundantly in the fall and summer as in the spring, and it is probable that many remain over winter in the pupal cavities. Those that come to the surface in autumn go into hibernation somewhat earlier than some of the other species and come out somewhat later. They appear in the latter part of April or early May, reach sexual maturity in about a month, lay eggs and die.

CICINDELA DUODECIMGUTTATA, subsp. REPANDA.

The life-history of *C. duodecimguttata* sub-species *repanda* differs from that of *C. purpurea* in that the adults reach sexual maturity later in the spring and the egg-laying is distributed over a longer period.

The eggs are a bright yellow, 2 mm. long, $\frac{9}{10}$ mm. in diameter at the narrow end and 1 mm. at the broad end. They are laid in May and June in sloping ground; sand is preferred. The larval holes are about 10 cm. deep, and their general direction is at right angles when in sloping surfaces and oblique when in horizontal surfaces.

This species is exceedingly difficult to rear. If conditions become a little unsatisfactory to the animals they leave their holes. All of a very large brood, reared to the second and third stages, were lost by their escaping from the box in which they were kept. Screen was tacked on the edge of the box and allowed to project inwards, but the larvæ were seen to crawl around this, clinging by their feet, their abdomens dangling in the air—a very interesting piece of gymnastics in view of the fact that Geo. Horn asserted in 1878 that the larvæ of the *Cicindelidæ* could not assume the straight horizontal position in which they are commonly figured. Many individuals upon leaving the burrows, were devoured by those still in their holes. Schaupp worked with this species and enlarged upon the necessity of having separate dishes to prevent the larvæ from devouring each other.

C. DUODECIMGUTTATA.

With the exception of the rearing of larvæ from the last larval stage to maturity, this species has not been studied in the laboratory. The life-history is shown by field observations to be like that of *repanda*; larvæ are usually found in humus or clay. A complete life-history, with the exception of the egg, has been taken in early August, from 10 square decimeters of ground.

C. TRANQUEBARICA.

The life-history is essentially the same as that of *C. purpurea.*

The eggs are laid in a variety of moist situations. The larvæ go to a depth of from 22 to 50 cm. The sides and anterior corners of the pronotum are not pigmented in larvæ of the third stage.

The imagoes undergo a series of colour-changes.

C. SCUTELLARIS aber. LECONTEI.

The life-history differs from that of *C. purpurea* but slightly. The eggs are laid in dry sand which contains a little humus. The adults do not appear as early in the spring and continue later in the summer. About seven per cent of the larvæ are parasitized by the larvæ of *Spogostylum anale*, Say, one of the

Bombyliidæ (Diptera). The holes of this species vary from 25 to 45 cm. in depth.

The imagoes undergo a series of colour-changes continuing to death.

Cicindela hirticollis.

This species reaches sexual maturity in July and deposits eggs in the level, white, wet sand of the beach of Lake Michigan. The third larval stage is reached by most individuals in the latter part of August and the early part of September. The larvæ live in straight, vertical burrows, 15 to 20 cm. in depth. They disappear very late in the fall (being found as late as the middle of October) and reappear in April. After storms they have been found crawling on the beach and after heavy rains have been found on the tops of sand dunes. This is due to the fact that they leave their burrows with every deviation from the optimum conditions. This makes them difficult to rear. They go into the prepupal stage from the first of June to the latter part of July, or even later.

The colour of the imagoes undergoes a series of changes; the insects come out of the soil before the changes are ended and the chitin hardened. This appearance begins in the second week of July while the hibernated ndividuals are still present; the beach then swarms with them. The old individuals gradually disappear as the number of new ones increases, so that the presence of the new brood cannot be noted by numbers.

The number continues about the same during the month of July, after which it gradually decreases. Individuals that can be recognized as fresh by the condition of their cuticula have been repeatedly brought into the vivarium. They soon go into the ground and do not come out. Repeated examination of the females at this time of the year has never shown a single one to contain eggs, nor have I seen any cases of copulation. While I have not succeeded in bringing any of these individuals through the winter, there is little doubt from these observations that the adults go into hibernation in two or three weeks after their emergence and remain there until the following June.

C. sexguttata.

The female lays the eggs (June or early July) in shaded sand or clay containing humus, more rarely in pure humus. The eggs are of a bright cream-yellow, 1·8 mm. long and 1 mm. in diameter. Most of the larvæ pass the winter in the last stage, a small number in the second stage. The only specimens that were reared went into the prepupal stage before the 15th of June (one year after the eggs were laid) and one was observed to pupate July 29th, six weeks after, and emerge August 7th. All that were observed went into the prepupal stage from June 11th to the 17th and all emerged between August 4th and 8th. None of them dug their way out, but were removed for examination.

C. sexguttata rarely appears in northern localities in the autumn and it is probable that it remains in the pupal burrows until spring, as does *C. campestris.* The species is reported as appearing both autumn and spring in some southern localities. At Chicago the adults appear during April and May, while in the western part of the geographic range of the species, they do not appear until late in June—after the heavy spring rains which soften the soil so that the imagoes can dig to the surface.

Cicindela punctulata.

The eggs are laid in relatively hard dry soil, usually humus, in the latter part of July. They are hatched in two weeks; the first larval stage lasting three weeks, and the second three weeks; the third being reached by the majority in September. After hibernation the larvæ feed from the middle of April until early June.

The larval burrows during the feeding season are 30 to 40 cm. deep. They are shallower in the summer just before the animals go into the prepupal stage. In many cases the larva is overtaken by the condition of helplessness which precedes pupation and pupates in the upper part of the burrow, the pupa standing on end; more often a pupal cavity is constructed (Pl. **24.** fig. 20). The prepupal and pupal stages are each from ten days to two weeks in length. The imagoes emerge after a few days, and if the ground is sufficiently soft, dig their way out and reach sexual maturity by the end of about three weeks. The adults do not hibernate.

C. lepida.

The animals sometimes copulate in the small burrows which they dig in the sand. The eggs are laid in the latter part of July. My only observation of the eggs or egg-laying was one case in which the female, on a warm morning, stood on a board in one of the cages and deposited an egg from the end of the partially extended ovipositor, letting it fall on the board; the egg was accidentally destroyed. It was of a deep cream-yellow and a little smaller than that of *repanda.*

The second stage is reached in the autumn, by almost all of a given population. This stage lasts until the following June or July, after the full-grown larvæ have gone into the prepupal stage. The larvæ feed in this stage (third) until late in the autumn and then hibernate, coming out about the first of May. Their burrows are from 60 to 90 cm. deep and are very small in all of the stages. A natural funnel is frequently formed at the mouth of the burrows due to the action of gravity on the dry sand (fig. 19). The holes of the last stages, which live for nearly a year, are closed and partially filled with sand for much of the time and the larvæ never appear well fed. The adults are small.

The pupal cells are long and curved and are shaped much like the burrow of *C. limbalis* (fig. 19). The larvæ enter the prepupal stage in the last half of May, emerge as adults in the latter part of June and reach the surface during the first few days of July. They reach sexual maturity in about two or three weeks ; the life cycle occupies two years.

CICINDELA CUPRASCENS.

After much labour and many fruitless trials, I have succeeded in rearing a few larvæ of this species to the second stage. They have never been found in the field, due no doubt to the fact that they make burrows that are ragged at the edge and are like those of many other animals.

In my cages the female after making very many holes in the sand, laid a few eggs (July). The first larval stage lasted about one month and individuals in the second lived until the last of October without change. The life-history is thus far entirely parallel with that of *C. lepida*, to which this species is regarded as being more nearly related than to any other species hitherto mentioned. The adults appear at the same time as those of *C. lepida*.

V. TAXONOMY.

Larvæ belonging to several genera of the *Cicindelidæ* have been described, but our knowledge of their characters is at present too meagre to make a key practicable. The following characterizations of the described forms may, however, prove helpful.

Mantichora has the first antennal segment thick and the others very slender (Kolbe), while in all of the remaining described genera the antennal segments taper gradually distalward. In *Amblychila* the second segment is as long as the others taken together (Geo. Horn). *Eucallia* and some species of *Collyris* (R. Shelford) have two ocelli on each side, *Amblychila* has one, and the remaining described forms four. McGillivray made no place in his key to the families of Coleopterous larvæ for larval *Cicindelidæ* with less than four ocelli on each side, and Kolbe does not state the number in *Mantichora* but implies that there are four. *Omus* and *Collyris* have three pairs of spines on the dorsum of the fifth abdominal segment. All are about of a length in *Collyris* ; the middle one is much the longest in *Omus*. *Amblychila*, *Megacephala*, and *Cicindela* never have more than two. In *Amblychila* the inner one is the longer, while in all of the others the outer one is the longer ; the inner may be absent.

The larvæ of the different species of *Cicindela* are difficult to distinguish. The habitat, the form of the burrow, and the size and colour of the head and the prothorax are good taxonomic criteria, but these do not suffice. The distribution and number of bristles on the dorsal side of the head and the prothorax of the larvæ of a given species are very constant. These, taken with the other criteria just mentioned, leave little chance of error in identifying the larvæ of the species considered in this paper. Plate **26**, figs. 25–58 shows the distribution of bristles on the head and prothorax of these species. The position of bristles that are sometimes absent is indicated by a ×.

The first larval stage of *C. purpurea* (fig. 25) shows the usual type of pilosity pattern of the first stage of the species here considered. The second stage (fig. 26) possesses more bristles than the first and the arrangement is here again very typical. The third stage (fig. 27) differs less from the second than the second does from the first. The pilosity pattern of the larvæ of *C. purpurea limbalis* does not differ in any essential particulars from that of *purpurea*. In the discussion of the succeeding species, attention will be directed chiefly to the prothorax, the head presenting less interesting differences in the different species.

The distribution of bristles in the first stage of *C. sexguttata* (fig. 28) is like that in the first stage of *C. purpurea*. The second stage may be distinguished from that of *C. purpurea* by the presence of the bristles Y and Z; the third by bristle Z alone. Leng placed *C. purpurea* and *C. sexguttata* in the same group; his contention is borne out by these larval characters. The first larval stage of *C. punctulata* (fig. 31) differs from the corresponding stage of the preceding species by the absence of bristle W (see fig. 28). This structure is present in the second stage (fig. 32) in which the bristles U and V are sometimes present also. The third stage (fig. 33) is subject to considerable variation, but in case the pilosity pattern duplicates that of the preceding species, the larva can always be distinguished by the size of its head (Table III.).

The first stage of the larva of *C. repanda* (fig. 34) lacks bristle W (see fig. 28), but possesses bristles T and V (see fig. 32). Bristles V and Z (see fig. 29) are usually present in the second and third stages (figs. 35 and 36). The distribution in *C.* 12-*guttata* (figs. 37–39) does not differ in any essential way from that in *C. repanda*. The bristles are usually larger and occasionally bristle S (fig. 39) is present.

The first stage of *C. generosa* (fig. 40) is like that of *C. repanda* (fig. 34). The second stage (fig. 41) lacks the bristle V. The third stage (fig. 42) is in some cases without those indicated by the ×. The first stage of *C. tranquebarica* (fig. 43) is like that of *C. repanda*. The second stage (fig. 44) possesses in addition to the bristles present in the second stage of *C. repanda* (fig. 35) bristle Y (see fig. 29). The third stage often (fig. 45) does not possess bristle Y.

The distribution in the first stage of *C. scutellaris* (fig. 46) is like that of the four preceding races. The second stage (fig. 47) differs from the second stage of *C. repanda* only in having bristle Y (see fig. 29). The third stage (fig. 48) possesses a number of bristles on each side of the median line of the prothorax.

The first stage of *C. lepida* (fig. 49) is like that of *C. repanda* except for the bristles on the anterior side of the head which may be weak or absent. The second and third stages (figs. 50 and 51) possess many bristles that have not been noted in any of the preceding species and races. These fall into longitudinal and cross lines of more or less definiteness which will be discussed in a succeeding paragraph.

The first larval stage of *C. cuprascens* (fig. 55) is like that of *C. lepida* (fig. 52), but the second stage is more like that of the last stage of *C. tranquebarica* (fig. 45).

In addition to the species herein treated, these characters have been examined in the larval stages of *Tetracha Carolina*, Linn., larvæ evidently belonging to African and Australian *Megacephalidæ*, in the British Museum, and of the following species kindly sent to me by Dr. Walter Horn, of Berlin :—*C. campestris*, Linn., *C. hybrida*, Linn., *C. maritima*, Dej. (?), and *C. biramosa*, Fabr. (Ceylon). The larger and more constant bristles of the American species of *Cicindela* are present in all these. *Tetracha Carolina*, Linn., has a pattern strictly comparable to that of *C. purpurea*, 12-*guttata*, etc. The pattern of some of the European species is identical with that of *purpurea*. The study of the distribution of these bristles is difficult and their development and relation to other morphological structures have not been studied. Any interpretation of their arrangement must accordingly be purely tentative and for convenience in further study.

The bristles fall with greater or less precision into several transverse and longitudinal rows. There are four pairs of longitudinal rows on the prothorax (A, B, C, and D of fig. 57) and two on the head (E and F of fig. 58). The principal transverse rows are 1, 2, 3, 4, 5, and 6 on the prothorax and 7, 8, 9, and 10 on the head. The positions of the principal bristles are indicated by the point of crossing of the lines. The positions of the more constant bristles are starred.

At the present time it is impossible to make a key as so few larvæ are known and, in the case of the described ones, no figures or descriptions of the arrangement of bristles have been presented. Accordingly, the distinguishing characters of the different stages and species are presented in the Tables below. For the arrangement of the bristles the reader is referred to the figures just described.

No generally practicable way of distinguishing the pupæ has been found. Excepting an occasional rudiment of some of the large and constant ones, the bristles are lost in the pupæ.

TABLE I.—Showing the characters of the first larval stages.

Species.	Width of prothorax.	Fig.	Coloration of head.	Coloration of prothorax.
purpurea	1·25 mm.	25	Shining blackish green.	Do. head.
limbalis	1·25 mm.	25	Blackish green with cupreous reflections.	Do. head.
sexguttata	1·5 mm.	28	Greenish black.	Do. head.
punctulata	·7–·9 mm.	31	Iridescent black.	Do. head.
repanda	1·2–1·5 mm.	34	Cupreous.	Do. head.
12-*guttata*	1·2–1·3 mm.	37	Cupreous.	Do. head.
generosa	1·5–1·75 mm.	40	Dull brown and pale brown (fig. 16).	Do. head.
tranquebarica	1·5–1·75 mm.	43	Greenish black.	More cupreous than head.
scutellaris	1·25–1·5 mm.	46	Dull green to purple.	Do. head.
lepida	·9–1·1 mm.	49	Shining black.	Dull black.
hirticollis	1·2–1·5 mm.	52	Reddish gold.	Do. head.
cuprascens	1·1 mm.	55	Greenish cupreous.	Do. head.

TABLE II.—Showing the characters of the second stages.

Species.	Width of prothorax.	Fig.	Coloration of head.	Coloration of prothorax.
purpurea	2 mm.	26	Dull black with cupreous reflections.	Do. head.
limbalis	1·5–2 mm.	26	Shining cupreous with greenish reflections.	Do. head.
sexguttata	1·75–2 mm.	29	Brown or blackish green.	Do. head.
punctulata	1·3–1·8 mm.	32	Iridescent black.	Do. head.
repanda	2 mm.	35	Cupreous.	Do. head.
12-*guttata*	1·8–2 mm.	38	Cupreous.	Do. head.
generosa	2–2·5 mm.	41	Dull brown to cupreous brown.	Do. head (see fig. 16.)
tranquebarica	2·25–2·5 mm.	44	Greenish black.	Dull cupreous.
scutellaris	2 mm.	47	Dark green to purple.	Do. head.
lepida	1·8–1·9 mm.	50	Shiny black.	Dull black.
hirticollis	2·5–3 mm.	53	Reddish gold.	Do. head.
cuprascens	1·9 mm.	56	Shining greenish cupreous.	Do. head.

TABLE III.—Showing the characters of the third stages.

Species.	Width of prothorax.	Fig.	Coloration of head.	Coloration of prothorax.
purpurea	3·5–4 mm.	27	Dull purplish black.	Do. head.
limbalis	3·35–5 mm.	27	Shining greenish cupreous.	Do. head.
sexguttata	3·5–3·75 mm.	30	Purplish black.	Do. head.
punctulata	2·4–2·8 mm.	33	Black.	Duller than head.
repanda	3–3·5 mm.	36	Cupreous.	Do. head.
12-*guttata*	3–3·5 mm.	39	Greenish cupreous.	Cupreous.
generosa	4·25–4·5 mm.	42	Dull brown (fig. 16).	Dull brown (fig. 16).
tranquebariea	3·5–4·2 mm.	45	Greenish black.	Dull cupreous, sides and ant. margin pale.
scutellaris	3·5–3·6 mm.	48	Variable, greenish black to purple, &c.	Do. head.
lepida	1·8–2 mm	51	Shiny black.	Duller than head.
hirticollis	3·25–4 mm.	54	Reddish gold.	Do. head.
cuprascens	Unknown.			

The lengths of the pupæ of the species herein considered are as follows :—

Purpurea, *purpurea* var. *limbalis*, and *sexguttata*, 11–12 mm. ; 12-*guttata*, 12-*guttata* var. *repanda*, 10–11 mm. ; *hirticollis*, 11–13 mm. ; *lepida*, 9–10 mm. ; *punctulata*, 8–9 mm. ; *tranquebarica* and *formosa* var. *generosa*, 14–16 mm. The pupa of *cuprascens* is unknown.

The first stages are much more nearly alike than the second and third. Some of the species add many more bristles in the last two stages than others. In spite of the general resemblance of the patterns of the different larval stages, the species fall into groups entirely different from those that have been made on the basis of adult characters. On the basis of the distribution of bristles in the adults, the species considered fall into the following groups :—Head and prothorax pilose—*generosa*, *purpurea*, 12-*guttata*, *tranquebarica*, *hirticollis*, *scutellaris*, ... , *cuprascens*, and *lepida*. Head bald, pronotum pilose on the sides only—*sexguttata* and *punctulata*. Yet the larval pilosity of the last two species is very near that of *purpurea*, *tranquebarica*, etc. While, as has been already stated, some taxonomists have placed *C. purpurea* and *C. sexguttata* in the same group, *C. lepida* and *C. scutellaris* have never been regarded as in any way related. The larvæ do not, however, differ so strikingly as do the adults.

The further study of these larval pilosity characters and a comparison with pilosity characters of the imagoes would no doubt lead to interesting results. A careful homologizing of the adult and larval areas bearing bristles must, however, be made before such a study can be carried far. It has been noted that bristles representing line A (fig. 57) are present in many representatives of the *Cicindela flexuosa* group, *Cicindela regalis* group, and a number of other unrelated species. The arrangement of bristles on the head and prothorax of *Ctenostoma* and some species of *Manticlora* appears to be definite, but its relation to the larval arrangement is not clear from casual inspection.

VI. Relation of Life-Histories and Habits to Environmental Factors.

A. *Hibernation.*

The physiological aspect of hibernation has not been studied in detail. Bachmetjew has performed extensive experiments on the temperature relations of insects, and has reported that the insect fluids do not freeze until a point in some cases as low as $-15°$ C. When the fluids freeze, the temperature rises to about $-1°{\cdot}5$ and the insect never regains life. The rapidity of thawing has no effect on this result; if cooled ever so low without freezing, the insect regains vitality. He suggests, in connection with hibernation, that the loss of water due to the insect's failure to feed for a long period in the late fall, causes an increased concentration of the body fluids which lowers their freezing-point. Greeley found that low temperature caused certain Protozoa to encyst or produce spores. Tower found that *Leptinotarsa* loses 30 per cent. of its weight, 3 per cent. excreta and 27 per cent. water, in preparing for hibernation, and was unable to prevent this preparation by experimental means in beetles that normally hibernate.

The larvæ of all species studied pass through at least one winter. With the approach of cold weather (late September) they dig their burrows deeper, piling the sand beside the opening in a single heap. They finally stop digging and close the mouth of the burrow with soil, go to the bottom and remain until spring (observed by Criddle, Günther, and Enock in the case of species not here considered). When brought into the vivarium and kept at 27°–30° C., they remain active for two or three weeks longer than out of doors. They finally close their burrows and go to the bottom, notwithstanding the higher temperature. Individuals fed continuously during the time they are kept under these abnormal conditions, were not notably influenced as to the time they closed their burrows. If the soil is kept dry they prepare for hibernation sooner than when it is very moist.

If the temperature be raised to 36°–40° C. and the soil and surrounding atmosphere kept moist, larvæ of *C. hirticollis*, *tranquebarica*, and *scutellaris* will nearly all go through their transformations without the winter rest and emerge as adults in December or January.

The adult beetles burrow into the ground for hibernation in the late summer or early autumn. Individuals of *C. repanda* have been found congregated in large numbers on sloping sandy surfaces in the middle of October. Their hibernation burrows are about 30 cm. in depth, going in obliquely for 15 cm. and then curving downward. The following depths were recorded for individuals of the following species, taken from a loamy-humus bank : *repanda*, 5–10 cm. ; *tranquebarica*, 15 cm. ; *purpurea*, 10–12 cm. ; *duodecimguttata*, 10–12 cm. Some of these were taken from the same burrow, and one of the burrows was evidently that of a carabid. Criddle has recently published an extensive paper describing the depth to which the adults dig and the method of digging.

The adults of species, e. g. *hirticollis*, which go into hibernation in early September are not affected by being placed in a warm vivarium. Adults which prepare for hibernation late in the autumn (*purpurea*, *scutellaris*, *tranquebarica*, etc.) may be delayed by high temperature. In all cases where high temperature continued, the individuals died in the soil or came out at the end of a month or more and died soon after.

It appears from these experiments that hibernation is a definite physiological process so well impressed on the species, that extreme stimulation is required to break it up.

B. *Temperature Relations.*

Under experimental conditions, the depth to which the larvæ of *C. purpurea limbalis* dig their burrows is related to the soil temperature (Table IV.)

TABLE IV.

	Temperature.			Average depth of burrow.
	Top.	6 cm. below.	10 cm. below.	
Moist	24° C.	22° C.	....	5·37 cm.
Dry..........	24° C.	22° C.	....	5·5 cm.
Moist	35° C.	....	33° C.	8·75 cm.
Dry..........	35° C.	....	33° C.	8·75 cm.
Moist	25° C.	24° C.	....	7·25 cm.

Lamp chimneys containing larvæ that had been in the cool moist conditions were transferred to the warm moist conditions. The larvæ at once excavated their burrows to depths comparable to those of the larvæ kept for some time in the *warm conditions*. One individual whose burrow was only 2 cm. deep, dug to a *depth* of 6·25 cm. in 28 hours, and to 10 cm. in 48 hours.

The pupal cells of *purpurea limbalis* are made by enlarging and sometimes shifting the inner end of the burrow (Pl. **24.** fig. 18). In the construction of the pupal burrows the same relations to temperature are shown as in the depth of burrows. Actual statistics were not preserved in the case of other species subjected to experimentel conditions, but observations on *scutellaris* and *tranquebarica* show that they respond to temperature in the construction of the pupal cells in the same way as *purpurea limbalis*. Under experimental conditions in which about 15 cm. of soil are heated (bottom 33°–39° C.; top 36°–41° C.) from above so as to give a difference of about one degree for each 7·5 cm. of depth, these species almost always constructed cells as near the bottom as possible. In cool conditions (bottom 22°; top 18°) cells are usually constructed near the top; none have been noted at the bottom. In view of these responses it is evident that marked differences in the depth of pupation may be brought about in a given brood of the same species by alternating short periods of warm and cool weather during the time of preparation of the cells. Individuals at *different depths would be subjected to very different conditions during their quiescent stages.*

In the habitat of *scutellaris* the temperature of the soil at 2.00 P.M. on a warm sunny day when the surface is dry, is about as follows:—Surface 47° C.; at a depth of 3·75 cm., 38°; 7·5 cm., 35°; 10 cm., 33⅓°; 12·5 cm., 32°; 17·5 cm., 30°. The surface of the soil is subject to the greatest extremes; the conditions become more constant, both in temperature and moisture, as we go downward.

Few observations have been made on the depth of pupation in nature; one pupa of *C. scutellaris* was found at a depth of 10 cm., while *C. tranquebarica* has never been observed. *C. punctulata*, which can be subjected to a temperature of 47° C. during the quiescent stages without fatal results or modification of the adults, pupates at a depth varying between 2·5 and 7·5 cm.

The length of the prepupal and the pupal stages is related to temperature. The process of development is probably most rapid when the temperature during the day averages about 28°–30° C. (the temperature at which most of the records here presented were made). At this temperature the length of the combined quiescent stages has been noted as usually from four to six weeks. If the temperature is lowered to 20° or 22° it is six to eight weeks, and if lowered to an average of 15° to 17° it will be increased to ten or twelve weeks. If the temperature be kept between 36° and 38° the time is increased to eight weeks.

The effect of cold on the development of colour is similar: lowering the temperature ten degrees in *C. limbalis* caused an increase of time for development to three or four times and in some stages of the development it stopped it altogether. Such influences of temperature on growth, respiration, &c., have been noted by various workers.

C. *Moisture Relations.*

As will be noted in Table IV., *purpurea limbalis* does not respond strikingly in the depth of its burrows to moisture conditions. The relations of the depth of burrows to the soil moisture in nature has been found not to be striking. The larvæ that have burrows near the ground water-level never go to a depth which would give actual water in their burrows, and accordingly may have shallow burrows. When above the ground water-level variations in depth are apparently not definitely related to soil moisture. Statistics on this point are very contradictory.

With the exception of the larvæ of *C. duodecimguttata*, its subspecies *repanda*, and *hirticollis*, the species described in this paper do not leave the spot where the female lays the eggs, except under very unusual circumstances, such as the complete flooding of the habitat. Only a small percentage of the individuals come out even under such conditions. When too dry, they close the burrow near the mouth and go to the bottom; here they remain inactive, and if bad conditions continue, finally die.

When placed in sand (clay being their natural habitat) and kept at a temperature of about 19° to 24° C., about 15 per cent. of the larvæ of *C. purpurea limbalis* will leave their holes. Probably not more than from 3 to 10 per cent. of the larvæ of the other species, with similar habitats, migrate even under the very artificial conditions of my experiments.

C. duodecimguttata, *repanda*, and *hirticollis*, on the contrary, leave their burrows often. If the soil becomes too dry, they come out and seek a place which is suitably moist. In captivity, when kept in separate receptacles whence they cannot escape, they leave the soil, if it is allowed to become too dry, and run around and around the side of the dish until they die from exposure and exhaustion. They cannot dig a new burrow in sand if the surface is dry.

These two species thus adjust themselves to conditions and are much less variable in many of their characters than other species. This is especially noticeable in the geographical variation. However, since the larvæ of *C. hirticollis* have been found in unusual positions such as the tops of sand dunes, after heavy rains, it is possible for them to be overtaken by dry conditions after they have become helpless in connection with pupation.

In moist conditions most of the species go through their transformations two or three days to a week sooner than in very dry conditions.

D. *Food.*

The food of the larvæ consists of land crustacea, centipedes, spiders, dragonflies, butterflies, flies, beetles, and larvæ of all sorts, in fact any small animals that come within reach. If the larvæ are not fed, they will not die for a week or two, or even longer, but the lengths of their periods of growth are greatly increased.

It has been noted that pupæ which emerge late in the season and which have been in the warm vivarium for a period of two or three months, are much smaller than those that appear at the usual time of the species. This is probably due to an acceleration of physiological processes without sufficient feeding.

As was pointed out in connection with the larvæ of *C. lepida*, the burrow is of such a type (Pl. **24**. fig. 19) that the sand closes it and the larva is unable to feed during much of the time. The larval life is two years and the imagoes are small. *C. generosa*, on the other hand, has an especial arrangement for keeping the burrow open (Pl. **25**. figs. 22–24), and the larval life is one year and the imagoes large. Whether or not this time difference is related to food conditions, is uncertain.

E. *Relation of Habits and Responses of the Adults to the Environmental Conditions of the Young Stages.*

1. *Sexual Maturity and Mating.*

None of the species which hibernate reach sexual maturity in autumn. If the eggs were laid at this time the larvæ would not be able to feed and store up enough food to enable them to withstand the winter conditions. The imagoes show no tendency to copulate until after a number of the warm days of spring have passed, and mating takes place only on warm and usually sunny days.

2. *Egg-laying.*

Species which lay in hard soils like humus or clay, are able to do so only when it is moist. Accordingly, during a dry period they select a place near a spring or brook where the moisture is adequate. On the approach of the wet weather, the larvæ will accordingly be subjected to extremely moist conditions or may be destroyed by high water or other disturbances. During a wet period such species lay in higher and dryer places. If a dry period follows, the larvæ will be subjected to extremely dry conditions, and if the surface of the soil becomes very dry soon after the laying of the eggs, the larvæ may not be able to make their way to the surface, and accordingly starve (see p. 161).

Species which lay in moist sand, after a rain may do so on the top of a dune, and the larvæ arising from such eggs be subjected to dry conditions later unless they make some adjustment.

VI. General Discussion.

We have noted that the imagoes of many species undergo a series of changes, particularly in colour, after they have appeared in their regular habitats; that in some species this change continues to the time of death; and furthermore that the two generations of *limbalis*, *generosa*, and particularly *hirticollis*, overlap so as to mix those that have just emerged with the old individuals that have hibernated. The importance of considering these facts in the study of variation need hardly be mentioned. Not to know the life-histories would lead to endless confusion in the study of geographical variation and of variation from generation to generation.

The possibility of differences in environmental conditions in the same brood of *Leptinotarsa*, due to periods of extreme weather, has been noted by Tower. In *Cicindela* we have two additional possibilities: (*a*) that of the pupal cells being constructed at very different distances from the surface by different individuals; and (*b*) of the entire larval life of some individuals being passed under unusual conditions because of the responses to the environmental peculiarities and necessary limitations in connection with egg-laying in the particular soil which a given species selects. Since the young stages of some species are sensitive, at least during the pre-pupal and pupal periods, to external stimuli, and since the results of such stimuli are manifest in modifications of colour and colour pattern, there is opportunity for soil temperature and moisture to influence variability.

Nor is this the only importance to be attached to these habits and responses. The animals select a definite place in which to lay their eggs and the larvæ of most species never leave their burrows. The migrating larvæ select a place themselves, and if it is not found soon, they die. All this leads to a definite distribution dependent upon the domestic habits and instincts of the species. This distribution I propose to call ecological distribution, from Haeckel's * definition of that term. Ecological distribution will be discussed in a succeeding paper.

VII. Summary.

1. The eggs are laid in open burrows made by the ovipositor as in the European species; the period of incubation is usually about two weeks. (pp. 160–161.)

* Ecology is the science of the domestic side of organic life, of the life needs of organisms and their relation to other organisms with which they live.—'Wonders of Life,' 1905.

2. There are three larval stages; the first usually lasts a little more than one month and the others vary greatly in different species. (p. 161.)

3. The burrows differ greatly in different species; *generosa* has a burrow which opens into the side of a pit, an adaption to shifting sand (p. 165); *cuprascens* does not smooth the edge of the burrow in the usual manner (p. 169).

4. The life-histories are of three types:—

(*a*) Eggs laid in the late spring or early summer; larvæ hibernate usually in the third stage, pupate in the second summer; imagoes emerge about a month after pupation, hibernate, and become sexually mature late in the third spring,—larval life lasts twelve to thirteen months, adult life ten months,—two years between generations. (pp. 161–167.)

(*b*) Eggs laid in mid-summer; larvæ hibernate usually in the third stage, pupate in the following June; imagoes emerge in early July and become sexually mature very soon,—larval life ten months, adult life two months,—one year between generations. (p. 168.)

(*c*) Eggs laid in mid-summer; larvæ hibernate in the second stage, reach the third stage early in the second summer, hibernate again, and pupate in the following May; imagoes emerge in the early part of the third summer and become sexually mature soon,—larval life twenty-one months,—adult life two months,—two years between generations. (pp. 168–169.)

5. Temperature, moisture, and food influence the length of the different stages. (p. 176.)

6. Pigmentation and final hardening of the cuticula take place in the pupa in those parts which are employed in the final ecdysis and the bristles of the imago assist in the removal of exuvium. (p. 163.)

7. The generations frequently overlap: of importance in connection with colour-changes to be discussed later. (pp. 164 & 167.)

8. The habits and responses of the imagoes and larvæ bring about great differences in the environmental conditions of different individuals of the same brood. (pp. 176–179.)

This work is a part of investigations which were begun at the Hull Zoological Laboratory, the University of Chicago, in 1903, and which are still being carried on with the facilities afforded by this institution. It gives me pleasure to acknowledge my indebtedness * to the staff of Zoology of this institution, for much kindly advice and enthusiastic encouragement.

September, 1907.

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Addenda.

While this paper was passing through the press, a description of the egg of *C. repanda* came to my attention. It was overlooked because it was included in an article entitled "Habits of *Cicindela*" (Moore). The eggs described must, however, have been abnormal. They were about one-half the size of the usual Cicindelid eggs. Only two were found and these were fastened together by some filaments. The chorion was sculptured and wrinkled, while in all other known eggs it is smooth. I have found that two or three undeveloped eggs are sometimes left in the ovarian tubules when the laying is ended; it is barely possible that the eggs observed by Moore were the last from an ovarian tubule. This, however, does not explain the sculpture.

Since this paper was written Bruch has published an account of the egg, larva, pupa, and adult of *C. apiata*, Dej. (South America). His article is concerned chiefly with pure description, but he expresses the opinion that there are two generations per year. He has, however, no good observations to establish this point. He figures the ovipositor, hole and egg, as well as the other stages described.

Dr. Walter Horn has a paper in the press in which he criticises R. Shelford's paper on *Collyris* and gives descriptions of the larvæ of a species of *Amblychila* and a species of *Omus*.

6th March, 1908. E. V. S.

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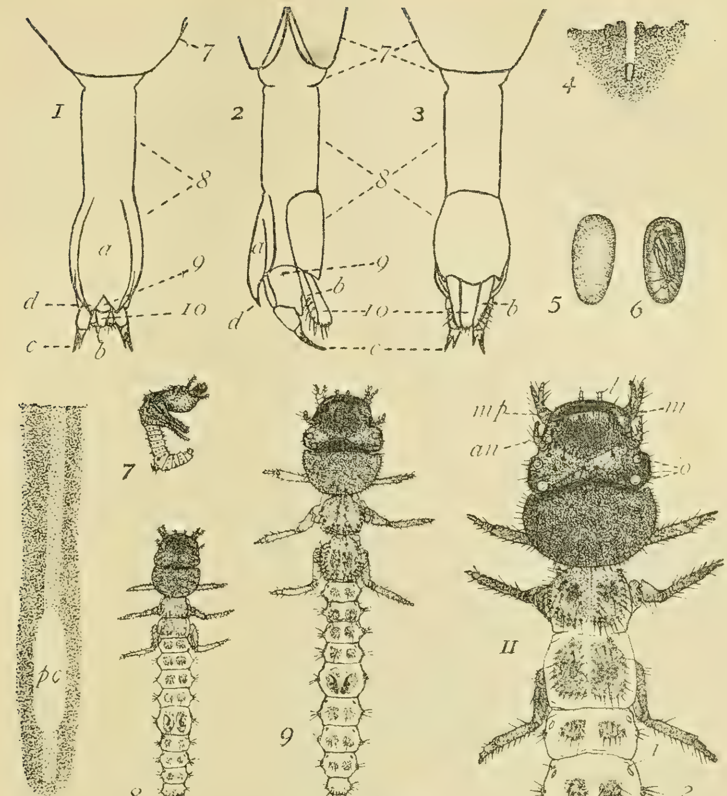
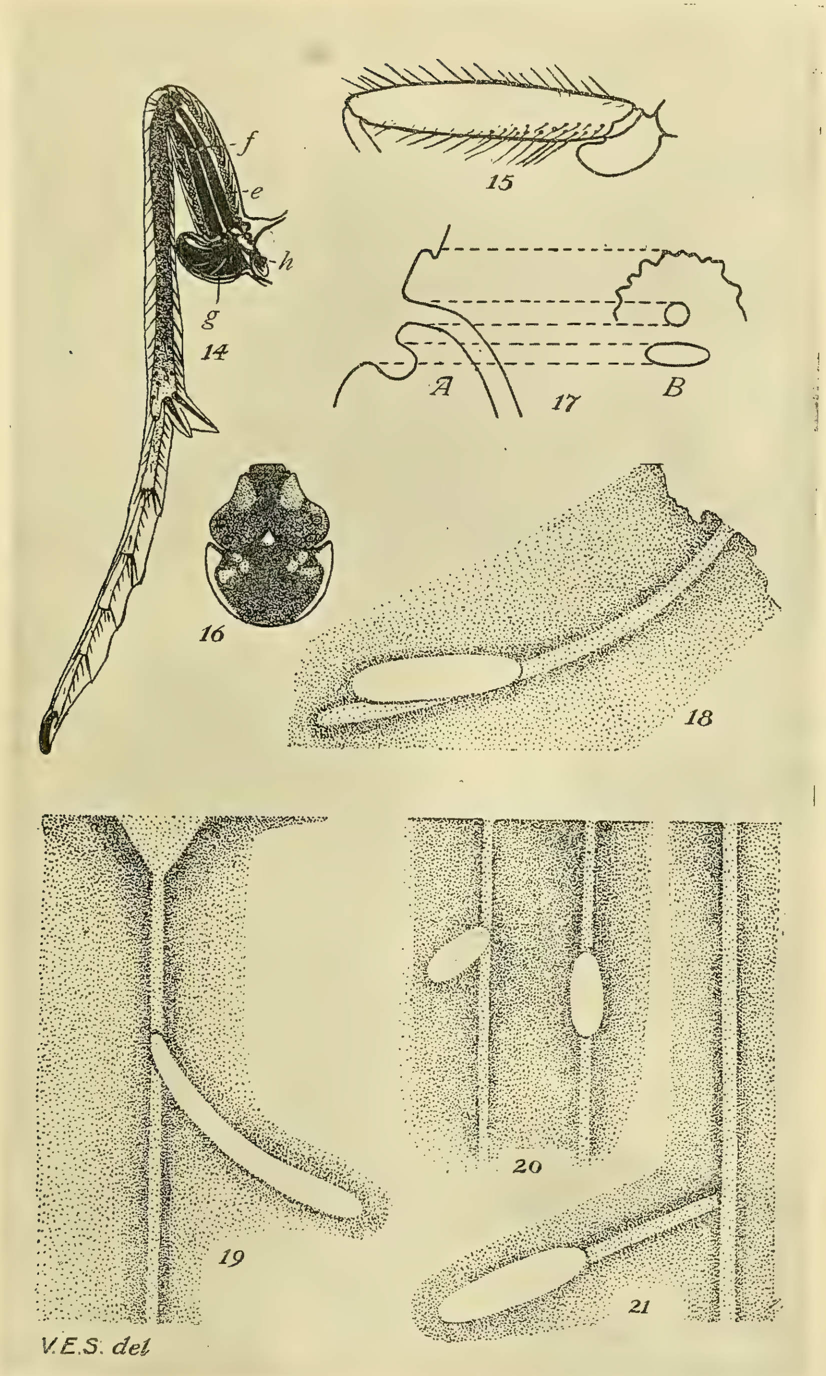


HABITS OF TIGER BEETLES.



HABITS OF TIGER BEETLES.

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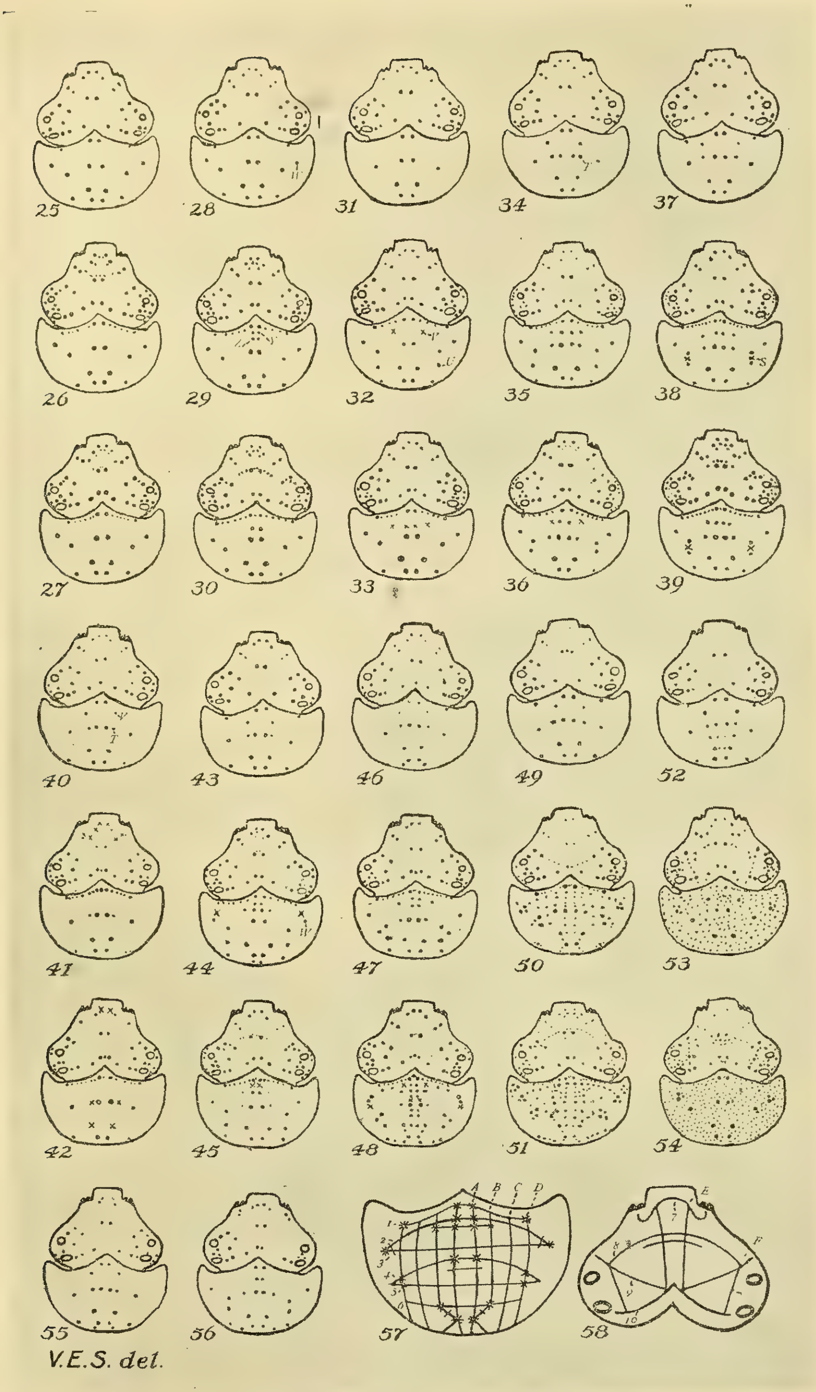
HABITS OF TIGER BEETLES.



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EXPLANATION OF THE PLATES.

PLATE 23.

Figs. 1–3. The ovipositor of *Cicindela purpurea.*

Fig. 1. Ventral view, × 4·5. Fig. 2. Side view. Fig. 3. Dorsal view.

a. Ventral chitinized plate. *b.* Outer gonapophysis of the 9th segment. *c.* Inner jointed gonapophysis of the 9th segment. *d.* Gonapophysis of the 8th segment.

Figs. 4–13. The life-history of *C. purpurea.*

Fig. 4. The egg in the ovipositor burrow, slightly reduced.
5. The egg at laying. × 4·5.
6. The egg just before hatching. × 4·5.
7. The larva at hatching. × 4·5.
8. The larva at the end of about two weeks. × 4·5.
9. The larva in the second instar. × 4·5.
10. Side view of the larva at the beginning of the third instar. × 4·5.
11. Full-grown larva. × 4·5.
12. Pupa. × 4·5.
13. The burrow and the pupal cell. × 0·4.

l. Labium. *m.* Mandible. *m.p.* Maxillary palp. *o.* Ocellus. *h.* Hooks. *an.* Antenna. *pc.* Pupal cavity.

PLATE 24.

Figs. 14 & 15. An appendage of *C. purpurea.*

Fig. 14. Leg within the pupal skin, showing the wrinkling of the femur and the large bristles arranged so as to assist in the removal of the exuvium. × 4·5.
e. Extensor tibiæ. *f.* Flexor tibiæ. *g.* Flexor femoris. *h.* Extensor femoris.
15. Femur extended, showing an adult length. × 4·5.

Fig. 16. Colour pattern of the head and pronotum of *C. formosa generosa.*
17. The burrow of *C. hybrida,* modified after Lesne.
A. Diagrammatic section; B. Front view.
18. The burrow and pupal cell of *C. purpurea limbalis.* The clear space represents the pupal cell and the faintly stippled part the old burrow. × 0·5.
19. The burrow and pupal cell of *C. lepida.* The funnel which is sometimes formed by the action of gravity on the dry sand is indicated. × 0·5.
20. The two types of pupal cell made by *C. punctulata.* × 0·5.
21. The pupal cell of *C. scutellaris.* × 0·5.

PLATE 25.

Fig. 22. A photograph of the head of *C. formosa generosa* in position at the mouth of the burrow. The pile of sand at the left is that thrown up by the animal.
23. A view of the same taken at an angle of 90 degrees to the direction of the former line of vision.
24. Photograph of the burrow opened so as to show a vertical section of both burrow and pit. (Photographs by V. E. S.)

PLATE 26.

This plate shows the distribution of the bristles on the dorsal side of the larval head and prothorax. The figures of the different stages and different species are all shown the same size to facilitate comparison.

Figs. 25–27. Represent respectively the three stages of the larva of *C. purpurea.*
28–30. Represent respectively the first, second, and third stages of *C. sexguttata.*
31–33. *C. punctulata.*
34–36. *C. repanda.*
37–39. *C. 12-guttata.*
40–42. *C. generosa.*
43–45. *C. tranquebarica.*
46–48. *C. scutellaris.*
49–51. *C. lepida.*
52–54. *C. hirticollis.*
55 & 56. *C. cuprascens.*
57 & 58. Show the principal lines of bristles on the head and prothorax.
A, B, C, D, E, F are the longitudinal lines; 1, 2, 3, 4, 5, 6, 7, 8, 9, 10 are the cross lines. Other lettering is only for convenience in the descriptions of the distribution. The most constant bristles are indicated in figs. 57 and 58 by the stars.